Distribution and Taxonomy of the Long-eared Bats, *Nyctophilus gouldi* Tomes, 1858 and *Nyctophilus bifax* Thomas, 1915 (Chiroptera: Vespertilionidae) in eastern Australia

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Although recently synonymized with *N. gouldi*, *N. bifax* is shown to be a distinct species separable on a number of external, cranial and bacula features. Cranial and external characters examined show that both species are similar in size, but can be readily identified in the field on the basis of fur colour, relative ear size, and details of the snout. Striking differences exist in external phallic morphology between each species.

Additional data on the distribution of *N. bifax* and *N. gouldi* have resulted from recent field work and a re-evaluation of material in Australian collections. The distribution of both species is summarized. The known distribution of *N. gouldi* is extended north by about 1100km to Atherton, north Queensland. *N. bifax* is recorded from a number of new localities south to Iluka, New South Wales, representing a southern range extension of some 750km. These species are therefore sympatric over 1600km in eastern Australia.

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INTRODUCTION

Six species of the australo-papuan bat genus *Nyctophilus* are generally recognized from Australia (Hall, 1984): *N. geoffroyi*, *N. timoriensis*, *N. gouldi*, *N. bifax*, *N. arnhemensis*, and *N. walkeri*. This paper considers the distribution and status of eastern Australian populations of *N. gouldi* and *N. bifax*, and is part of a continuing taxonomic study of *Nyctophilus*.

Historically, the taxonomic status of *N. gouldi* has been subject to controversy. Tomes (1858) described *N. gouldi* from specimens from Moreton Bay, Queensland, and Bathurst, New South Wales. Iredale and Troughton (1934) considered *N. gouldi* to be a southeastern Australian subspecies of the widespread *N. timoriensis*. Tate (1952) regarded *N. gouldi* to be a distinct species. However, until recently the arrangement of Iredale and Troughton (1934) has been followed by most authors. There is now general agreement that *N. gouldi* and *N. timoriensis* are distinct species (Hall and Richards, 1979; Allison, 1982; Koopman, 1984) and are known to be sympatric at several localities in eastern Australia (Parnaby, unpublished). Richards (1983) summarized the known range of *N. gouldi* as southwestern Western Australia, Tasmania, Victoria, eastern New South Wales and southeastern Queensland as far north as Bundaberg.

Thomas (1915) described *N. bifax* based on material from the Torres Strait islands and north Queensland. As of 1983, *N. bifax* was recorded from northern Western Australia, the Northern Territory and across to northeastern Queensland as far south as Sarina (Allison, 1983). Within this range, two subspecies are commonly recognized: *N. bifax bifax* from Queensland, and *N. b. daedalus* from the Northern Territory and Western Australia.

Koopman (1984) believed that the criteria proposed by Thomas for the separation of *N. bifax* from *N. gouldi* were not of sufficient magnitude to warrant species status and,

in view of the wide separation of their then known distribution, he tentatively placed *N. bifax* as a subspecies of *N. gouldi*. Based on the distribution data of Hall and Richards (1979), Koopman (1984) believed that the distribution of *N. bifax* and *N. gouldi* were separated by approximately 1000km in eastern Australia.

Koopman (1984), uncertain about the status of *daedalus*, placed it with *N. gouldi*, thereby tentatively proposing a single species with three allopatric subspecies: *N. gouldi gouldi* from southern Australia (but not Tasmania), *N. gouldi bifax* from north Queensland and *N. gouldi daedalus* from northern Western Australia and the Northern Territory.

Churchill *et al.* (1984) record a considerable southern extension of the known range of *N. bifax*, to the Pilbara region of Western Australia, and to Rockhampton in Queensland, thus closing the gap in the known range of this species and that of *N. gouldi* to approximately 1000km in Western Australia, and some 300km in Queensland.

Field work conducted by the author and others over the last five years, combined with a reexamination of existing Australian research collections, has resulted in further insight into the taxonomic status and distribution of these taxa. Morphologically, *N. gouldi* and *N. bifax* have been found to be readily distinguishable, both in the field and by examination of preserved material. This has facilitated the recognition of many new locality records including major range extensions of both species. Significantly, electrophoretic analysis of tissue samples collected from areas of sympatry in eastern Australia has provided unequivocal evidence of the distinct separation of *N. bifax* and *N. gouldi* (M. Adams and P. Baverstock, *pers. comm.*).

In this paper, the distribution of each species is summarized and new distribution records are presented which indicate large scale sympatry between *N. bifax* and *N. gouldi*. The major external, cranial and bacula features useful for distinguishing each species from throughout their range in eastern Australia are discussed.

Abbreviations used for research collections from which material has been examined are: Australian Museum, Sydney (AM); Australian National Wildlife Collection (CSIRO), Canberra (CM); Museum of Victoria, Melbourne (MV); South Australian Museum, Adelaide (SAM); Queensland Museum, Brisbane (QM) and Western Australian Museum, Perth (WAM).

Distribution

N. gouldi

As noted above, this species is recorded from southwestern Western Australia, Victoria through eastern New South Wales, to southeast Queensland (Richards, 1983). Richards also records this species from Tasmania but the specimens on which this is based belong with the large Tasmanian form of *N. geoffroyi* (see Discussion).

Previously, the most northern record of this species in eastern Australia was from near Gin Gin, Queensland (Thomas, 1915). Examination of museum material, and recent field collecting, have resulted in a substantial expansion of the known range to Atherton, 1100km north from Gin Gin.

The known distributional limits of *N. gouldi* in eastern Australia are shown in Fig. 1a and localities are listed in Appendix 1. The species is usually considered to be an inhabitant of mesic eucalypt forests of the Great Dividing Range. Hall and Richards (1979) record the species from inland southern Queensland. Additional records presented here from inland Queensland and New South Wales and field work in New South Wales indicates that *N. gouldi* is widespread and probably more common throughout lower rainfall regions than was previously realized. Thus this species appears to

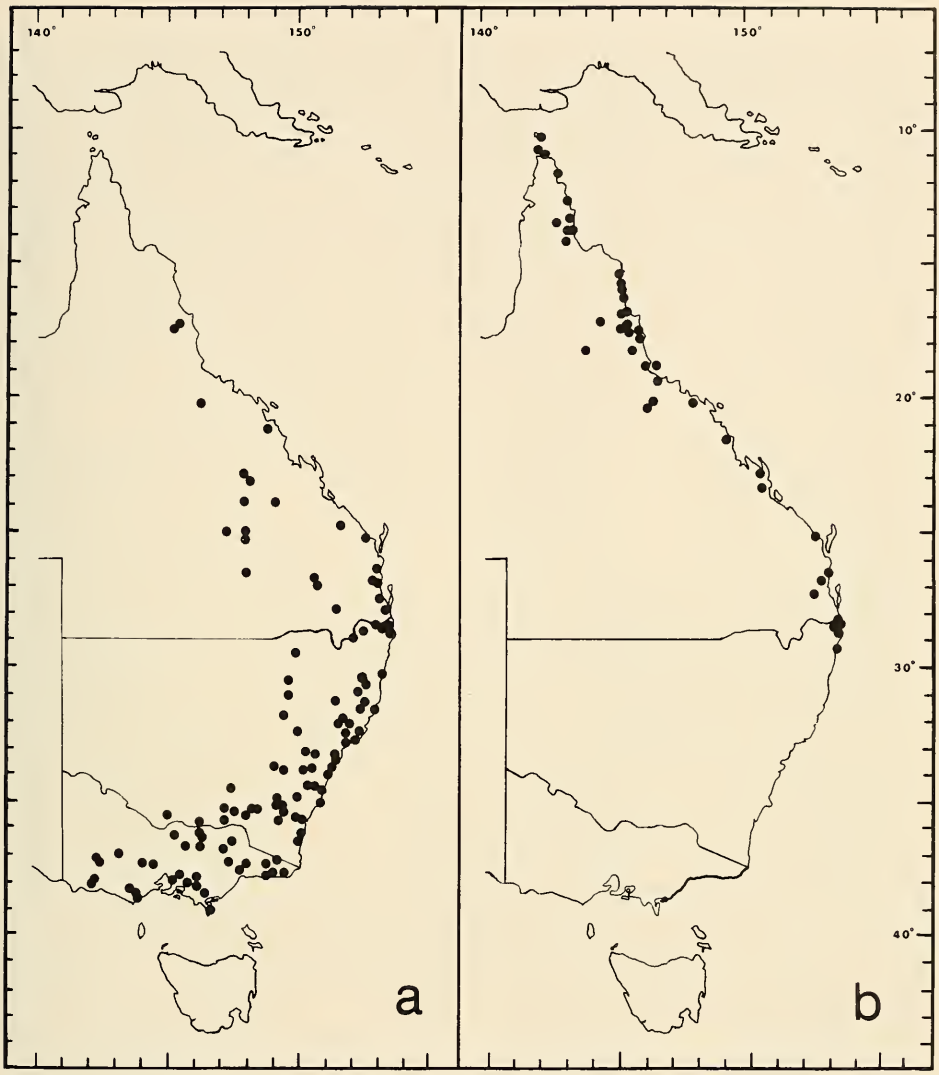

Fig. 1. Distribution of a, *N. gouldi* and b, *N. bifax* in eastern Australia.

occur in a range of habitats, including semi-arid woodland (such as in the Charters Towers region), brigalow country and sclerophyll forest.

N. bifax

The original description of *N. bifax* by Thomas (1915) was based on material from localities ranging from Torres Strait islands, south to Herberton and west to Cloncurry, northwestern Queensland. In eastern Australia, there are few published records of *N. bifax* south of Townsville; Allison (1983) depicts this species as extending south to about Sarina and Churchill *et al.* (1984) record *N. bifax* at Byfield, near Rockhampton. Examination of museum material, some of which had previously been misidentified, has resulted in a number of additional locality records in near coastal areas extending south from Townsville to southern Queensland.

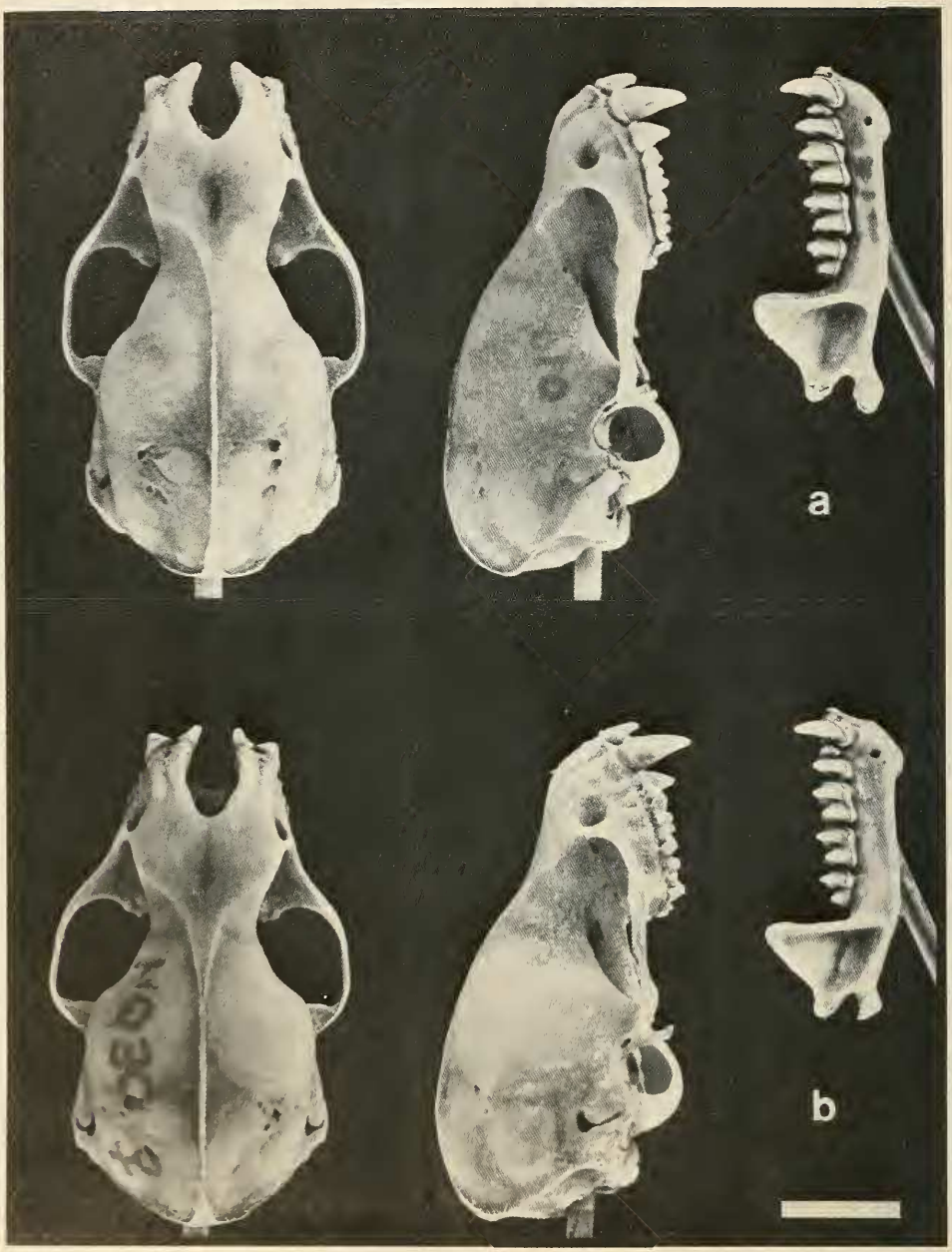

Fig. 2. Dorsal and lateral views of the skull and lateral view of the dentary of a, *N. gouldi* from Brisbane (QM JM5366, female); b, *N. bifax* from Atherton, Qld (AM M16181, female). Bar represents 4mm.

During field work in north coastal New South Wales, *N. bifax* was one of the most frequently trapped species of insectivorous bat. It was captured at low elevations at a number of localities as far south as Iluka (Parnaby, 1986), which is currently the most southern record for the species.

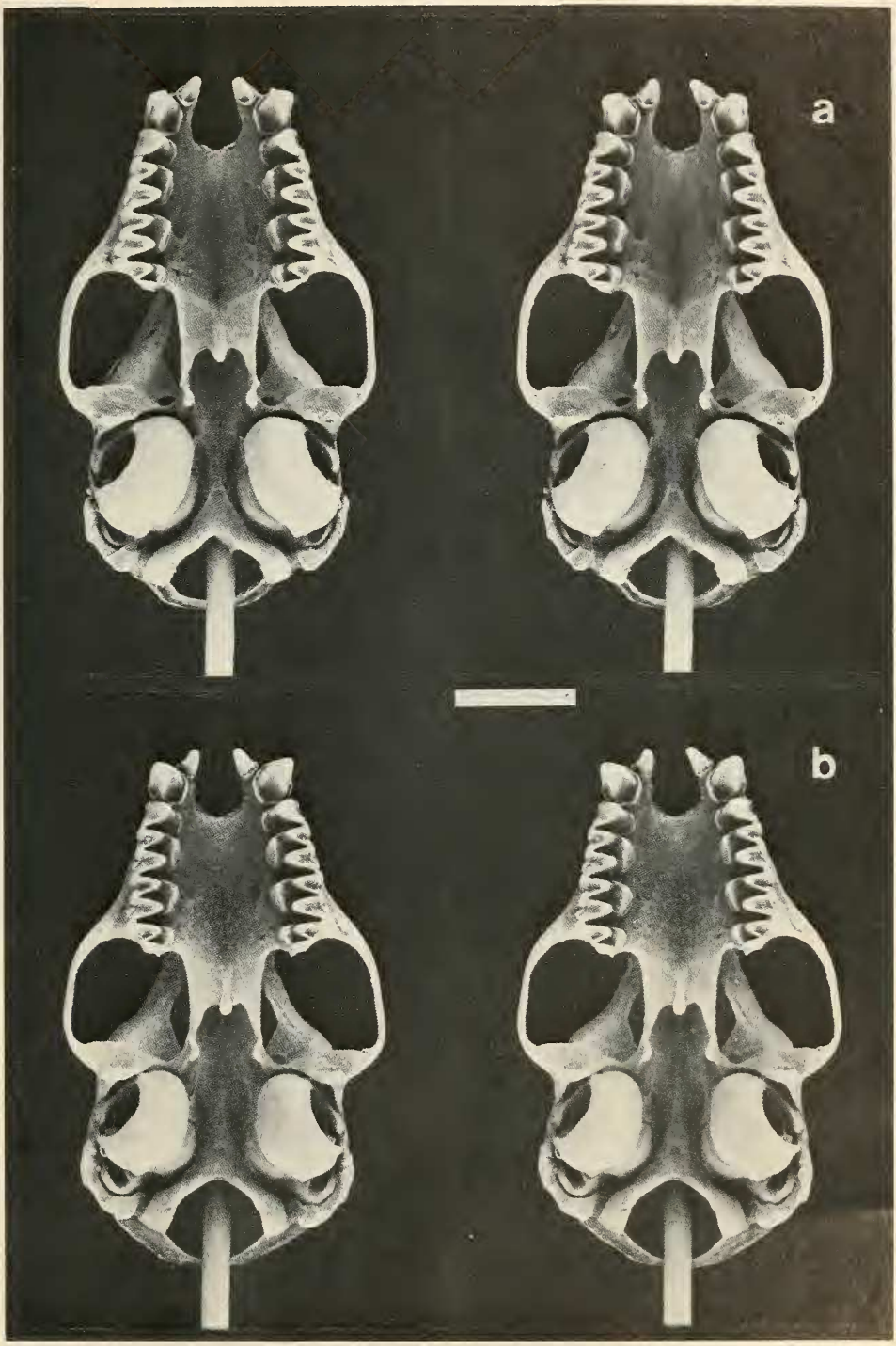

Fig. 3. Stereopairs of ventral view of **a**, *N. gouldi* from Brisbane (QM JM5366 female); **b**, *N. bifax* from Atherton (AM M16181, female). Bar represents 4mm.

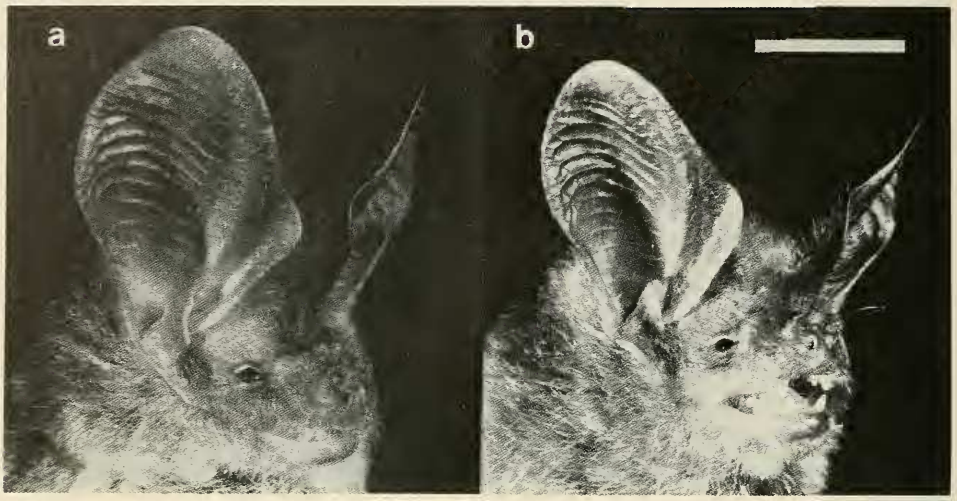

Fig. 4. Photographs illustrating differences in relative ear size between males of **a**, *N. gouldi* from Broken Head, N.S.W. (AM M13389) and **b**, *N. bifax* from Brunswick Heads, N.S.W. (AM M13388). Bar represents 1cm.

The updated distribution of *N. bifax* in eastern Australia is shown in Fig. 1**b**, and localities are listed in Appendix 1. With the exception of a specimen from the Cloncurry area (20° 42′S, 140° 30′E) reported by Thomas (1915) and one from the Einasleigh River (18° 11′S, 144° 00′E, AM M13356), most records are close to the coast. Allison (1983) notes the occurrence of this species in a variety of habitats ranging from rain forest to dry sclerophyll woodlands.

Morphological Differences

Substantial between-locality variation exists within each species throughout eastern Australia, particularly so in *N. gouldi* (see 'Metric variation' below). Despite this, diagnostic external and cranial criteria discussed in the following sections appear to hold, irrespective of locality.

Skull morphology

Compared with *N. bifax* the skull of *N. gouldi* is relatively narrow for its length, and is more slightly built (Fig. 2). In *N. gouldi* the bullae are relatively much larger, and consequently appear to be closer together medially (Fig. 3). The hamular processes of the pterygoids are slightly more ossified in *N. gouldi*. The paroccipital processes are slightiy more pronounced in *N. bifax* and are more clearly distinct from the occipital condyles.

The upper canines are laterally splayed in *N. bifax* yet in *N. gouldi* they are usually in line with the upper tooth row, however, occasional specimens of *N. gouldi* with splayed canines have been observed.

Like the skull, the dentary of *N. gouldi* is more delicately built and is shallower. The upward inflection of the postero-ventral border of the ramus is more marked in *N. bifax* and the angular process is generally shorter than that of *N. gouldi* (Fig. 2).

External Morphology

The most obvious external differences between these two species are in the relative size of the ears and general fur colour. Relative to body size, the ears are very large in *N. gouldi* (Fig. 4), while in *N. bifax* they are distinctly shorter.

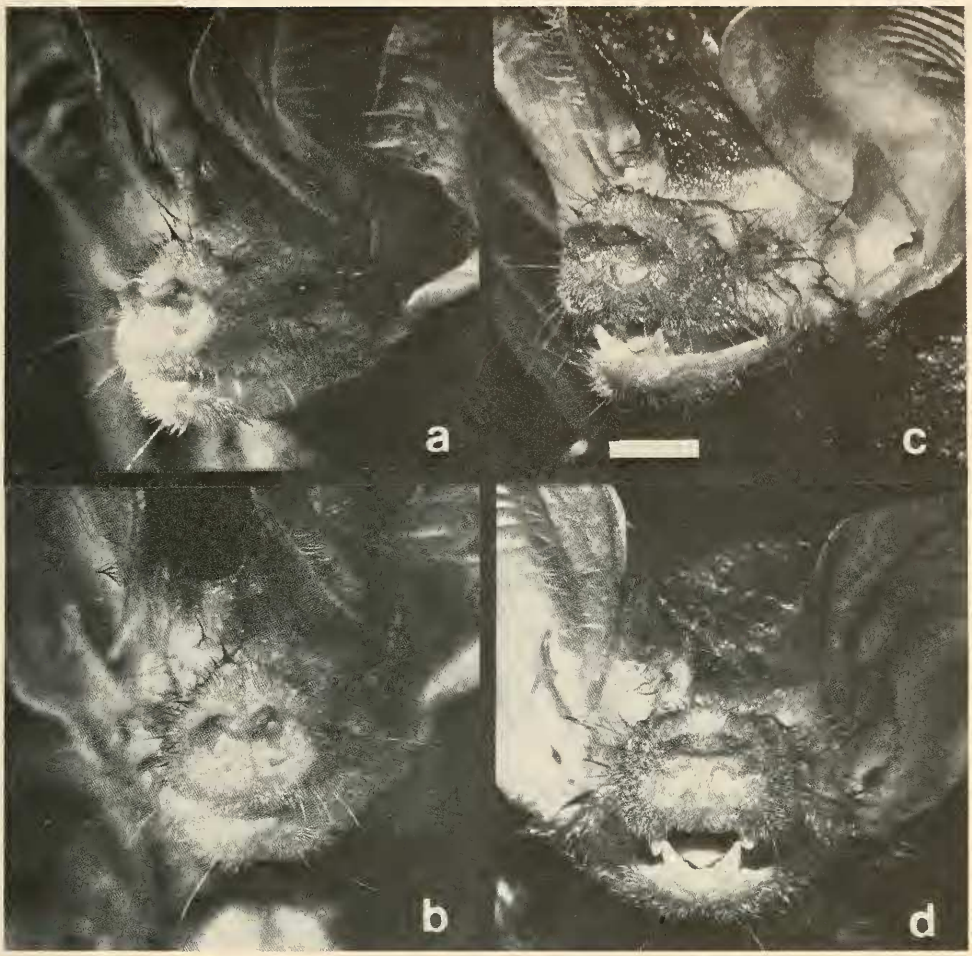

Fig. 5. Frontal and frontolateral views of the snout of **a**, and **b**, *N. gouldi* from Border Ranges, N.S.W. (AM M13412, male); **c**, and **d**, *N. bifax* from Brunswick Heads (AM M13388,male), showing differences in the post-nasal prominence. Bar represents 4mm.

From field observations, the dorsal pelage of *N. gouldi* is predominantly a slate grey or grey-brown with ash-grey ventral fur often mottled with very light buff. In *N. bifax*, the dorsum is light brown or tannish, with a lighter tannish undersurface.

There is a consistent difference in the shape of the post-nasal bump, as originally noted by Thomas (1915). Relative to the noseleaf, this structure is more developed in *N. gouldi* than *N. bifax* (Fig. 5) and in *N. gouldi* has a faint vertical groove which is weaker or absent in *N. bifax*. The specimens illustrated in Fig. 5 differ in the shape of the dorsal margin of the noseleaf; there is a median concavity in *N. gouldi* while the margin of *N. bifax* is evenly convex. However this difference is not diagnostic as the shape of the noseleaf is variable in both species.

Camera lucida drawings of a representative glans penis of an adult of each species are shown in Fig. 6. Each species differs in a number of obvious features. The lateral surfaces in *N. gouldi* are constricted in the mid-line, dividing the penis into a distinct

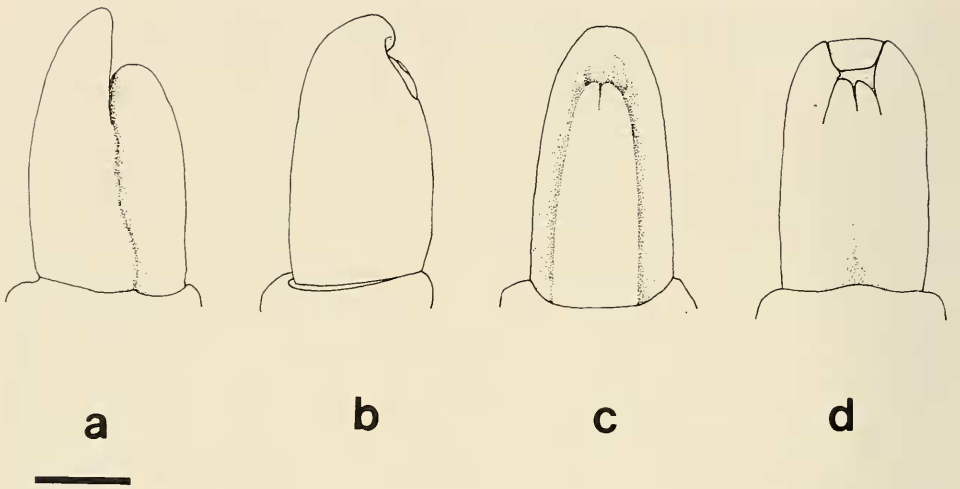

Fig. 6. Camera lucida drawings of the glans penis with prepuce removed. Lateral view of **a**, *N. gouldi* from Border Range, NSW (AM M13412), **b**, *N. bifax* from Brunswick Heads, NSW (AM M13388). Ventral view of **c**, *N. gouldi* and **d**, *N. bifax*. Bar represents 1.0mm.

dorsal and ventral element. The dorsal element forms a very distinct distal 'beak'. In marked contrast, the penis of *N. bifax* is approximately cylindrical, and the head of the penis is more truncated. Consequently, each species has a very characteristic profile which is clearly visible to the unaided eye.

Bacular morphology

As noted by Thomas (1915) *N. bifax* differs from *N. gouldi* in bacular morphology: in *N. gouldi* the baculum comes to a simple point distally whereas in *N. bifax* the tip is bifurcated by a crescentic notch.

Using X-ray photography, I have examined bacula from 17 specimens of *N. bifax* from localities scattered throughout the complete eastern Australian range of this species, from Iluka north to Lockerbie Scrub. The bifid condition is present in every specimen. Likewise, the sharp distal point is present in all 25 examples of *N. gouldi* examined from widespread locations throughout Victoria, New South Wales and Queensland. Thus, the condition of the distal tip of the baculum appears to be monomorphic in each species.

Metric Variation

A univariate and multivariate analysis of metric variation using analysis of variance, principal components analysis and canonical variates analysis of these and other species of *Nyctophilus* is in progress, and preliminary findings are outlined here.

Ten external dimensions were taken from 130 spirit-preserved specimens of *N. gouldi* from central and northern New South Wales and Queensland, and 118 spirit specimens of *N. bifax bifax* from throughout Queensland and northern New South Wales (listed in Appendix 1). Twelve cranial measurements were made on 69 skulls of *N. gouldi* and 52 of *N. bifax bifax*, all from throughout New South Wales and Queensland.

Sexual size dimorphism was found in the majority of dimensions in both species, with females on average larger than males. Consequently, sexes were treated separately in all analyses.

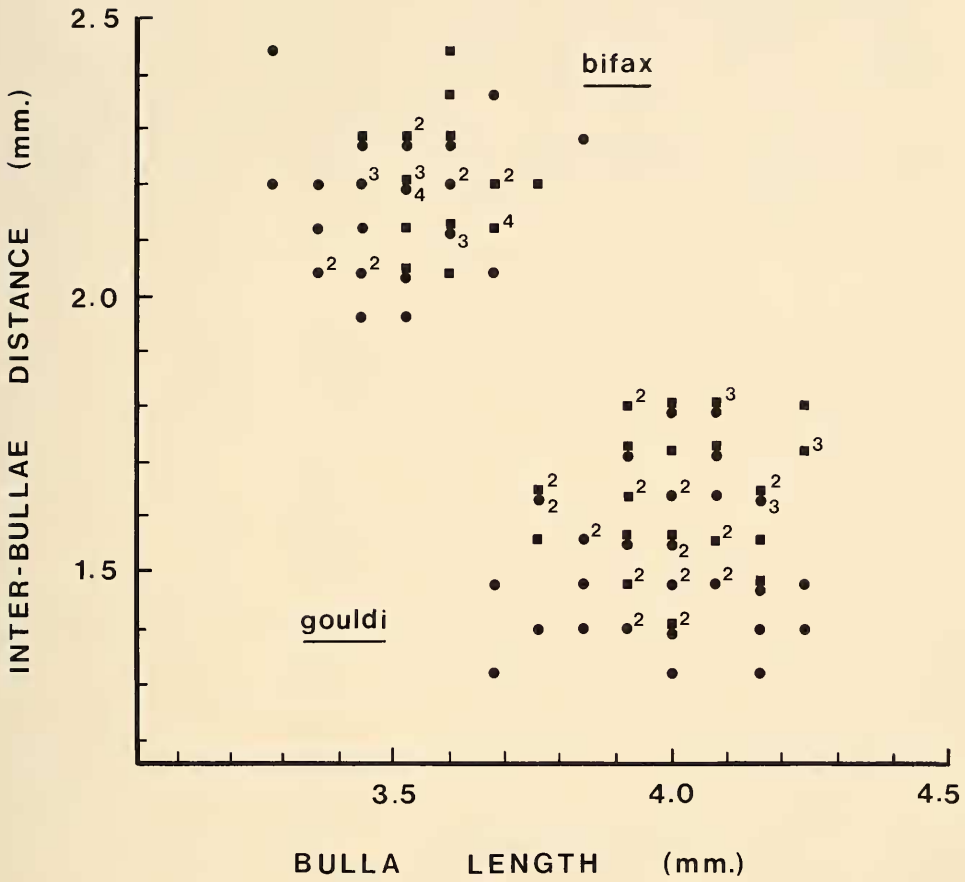

Fig. 7. Plot of interbullae distance (mm) against bulla length (mm) for 65 *N. gouldi* and 50 *N. bifax* from central and northern NSW and Qld. Both dimensions were measured in ocular units with a dissecting microscope, and the axes converted to mm. Circles represent males, squares females. Numerals indicate overlapping points.

When specimens from all localities are pooled, mensural ranges overlap between each species for all external and all but one of the 12 cranial and dental dimensions. Measurements with overlapping ranges are: ear length, measured from the notch; length of first digit; forearm length; third digit: length of metacarpal I, length of metacarpal II, length of metacarpal III; fifth digit: length of metacarpal I, II, and III; length of hind-leg; condylobasal length; greatest length of skull; length of upper tooth row (C^1-M^3); zygomatic breadth; interorbital constriction; outer breadth of upper third molars; height of braincase; skull breadth at mastoids; interbullae distance; bulla length, and basicranial length (measured from the anterior margin of foramen magnum to the anterior border of the posterior palatal emargination).

Interbullae distance is the only measurement in which the range for each species do not overlap: the range for *N. gouldi* being 2.0–2.5mm (n=65) and *N. bifax* 1.3–1.8mm

(n = 50). A plot of this dimension against bulla length for all localities combined (Fig. 7) results in a clear separation of *N. bifax* and *N. gouldi*.

In both species substantial size differences were found between localities. Although analysis of these data is preliminary, observed variation seems to correspond with local climatic conditions. This is evident in a plot of forearm length against longitude for samples of *N. gouldi* from diverse sites throughout New South Wales and Queensland (Fig. 8), where increasing longitude approximates decreasing aridity. For example, mean forearm length of a sample of female *N. gouldi* from a dry inland site (Pilliga Scrub, NSW) is 38.7mm compared with 45.8mm for females from a higher rainfall site in the Great Dividing Range at a comparable latitude (Doyles River State Forest).

The between-locality size variation evident in both species might be expected to obscure differences present within a given locality. In an attempt to reduce these locality

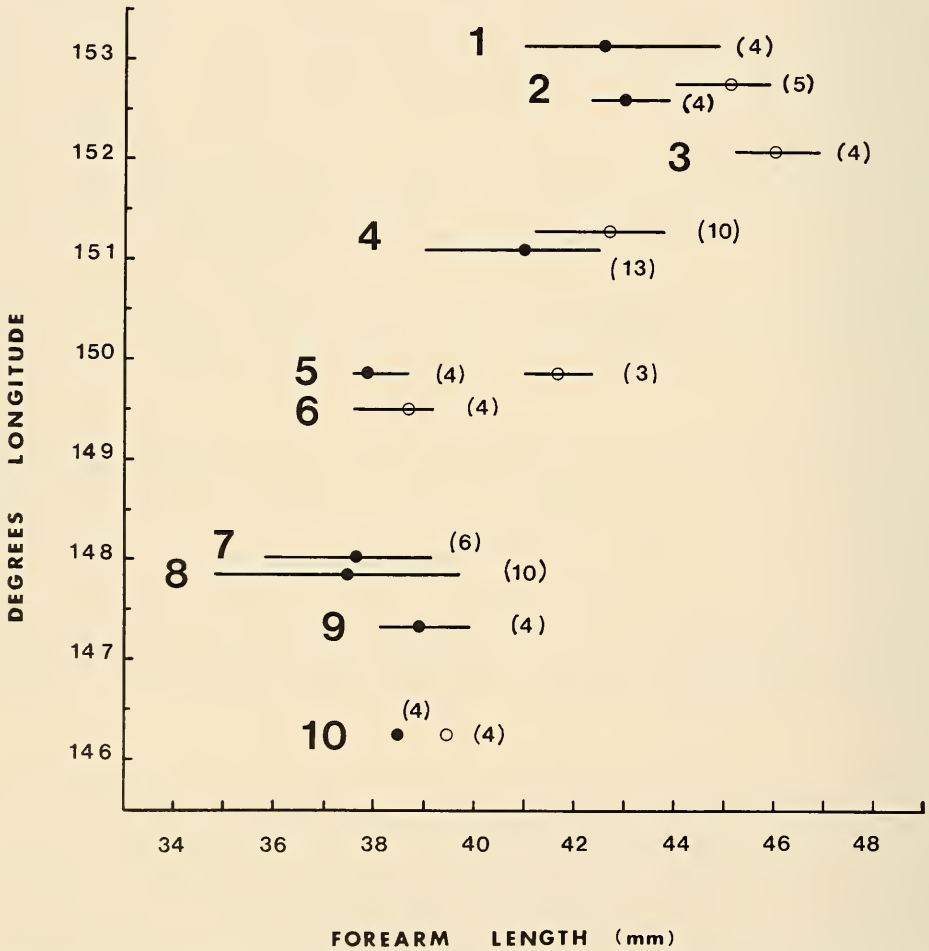

Fig. 8. Forearm length (mm) of *N. gouldi* versus longitude for samples from throughout NSW and Qld showing a trend of increase in size with longitude. Circles represent female sample means, dots male samples. Lines indicate sample range, sample size in brackets. Localities are, **1.** Tweed Rge, northern NSW; **2.** Gloucester Tops, central NSW; **3.** Doyles River State Forest, central NSW; **4.** Olney State Forest, central NSW; **5.** Cassilis region, central NSW; **6.** Pilliga State Forest, northern NSW; **7.** Tambo region, south-central Qld; **8.** Capella, central Qld; **9.** Henty region, southern NSW; **10.** Mt Leysham, north Qld. (from Churchill *et al.*, 1984).

effects, measurements of specimens from a restricted geographic region were compared. The only area of sympatry for which specimens are available in any numbers is north-eastern New South Wales and far southeast Queensland. Twenty-six specimens of *N. gouldi* and 23 of *N. bifax* were examined from localities ranging from the Conondale Ranges, south to Iluka in New South Wales and inland to Tooloom. Only three of these specimens are from north of Brisbane.

Measurements of spirit specimens from within this region were pooled by sex for each species. Summary statistics for external dimensions of each species are given in Table 1, and dimensions of 19 skulls of *N. gouldi* and 11 of *N. bifax* from the same region are given in Table 2.

TABLE 1

Summary statistics for external dimensions (mm) of spirit specimens of N. bifax *and* N. gouldi *from northern N.S.W. and southeastern Qld*

Sample sizes for all dimensions are: *N. bifax* (9 males, 14 females), *N. gouldi* (10 males, 8 females)

		MEAN	S.E.	S.D.	RANGE	CV
EAR LENGTH	MALES					
	bifax	24.78	.43	1.29	21.9–26.7	5.20
	gouldi	28.33	.44	1.40	25.8–30.0	5.78
	FEMALES					
	bifax	25.16	.24	.90	23.5–26.3	3.58
	gouldi	28.55	.29	.81	27.5–30.1	2.83
FOREARM	MALES					
	bifax	41.46	.34	.10	39.3–42.5	2.42
	gouldi	42.24	.43	1.35	39.5–44.9	3.62
	FEMALES					
	bifax	42.98	.23	.87	41.0–44.4	2.06
	gouldi	43.16	.52	1.46	41.2–45.2	3.38
DIGIT I	MALES					
	bifax	6.79	.089	.27	6.3–7.1	4.12
	gouldi	6.50	.11	.35	6.1–7.1	7.67
	FEMALES					
	bifax	6.94	.064	.24	6.6–7.3	3.46
	gouldi	6.87	.52	.42	6.0–7.3	6.11
DIGIT 3, METACARPAL I	MALES					
	bifax	38.99	.32	.95	37.5–40.5	2.44
	gouldi	39.92	.60	1.89	35.8–42.7	4.73
	FEMALES					
	bifax	39.74	.22	.84	37.7–41.0	2.11
	gouldi	40.66	.46	1.31	39.2–42.5	3.22
DIGIT 3, METACARPAL II	MALES					
	bifax	15.61	.15	.46	14.9–16.3	2.95
	gouldi	15.61	.19	.59	14.7–16.3	3.78
	FEMALES					
	bifax	15.93	.14	.51	15.1–16.9	3.20
	gouldi	16.30	.30	.84	15.2–18.0	5.15
DIGIT 3, METACARPAL III	MALES					
	bifax	14.61	.11	.33	14.0–15.1	2.26
	gouldi	14.09	.22	.70	12.5–15.0	4.97
	FEMALES					
	bifax	14.66	.12	.43	13.8–15.2	2.93
	gouldi	14.14	.34	.96	12.9–15.8	6.79

TABLE 1 (continued)

		MEAN	S.E.	S.D.	RANGE	CV
DIGIT 5, METACARPAL I	MALES					
	bifax	38.91	.32	.95	37.4–40.7	2.44
	gouldi	39.74	.46	1.45	37.2–42.6	3.65
	FEMALES					
	bifax	40.01	.21	.80	38.8–41.4	2.00
	gouldi	40.52	.52	1.46	38.9–42.8	3.60
DIGIT 5, METACARPAL II	MALES					
	bifax	10.58	.12	.37	10.0–11.2	3.50
	gouldi	10.91	.17	.54	10.2–12.2	4.95
	FEMALES					
	bifax	10.84	.072	.27	10.4–11.4	2.49
	gouldi	11.43	.22	.62	10.6–12.2	5.42
DIGIT 5, METACARPAL III	MALES					
	bifax	10.71	.20	.61	9.4–11.5	5.69
	gouldi	10.00	.27	.78	9.0–12.0	7.80
	FEMALES					
	bifax	10.51	.19	.71	8.4–11.4	6.75
	gouldi	10.01	.27	.78	8.9–10.9	7.79
HINDLEG LENGTH	MALES					
	bifax	21.67	.16	.48	21.0–22.3	2.21
	gouldi	20.78	.27	.82	19.7–22.1	3.95
	FEMALES					
	bifax	21.90	.11	.42	21.2–22.7	1.92
	gouldi	21.20	.34	.95	19.8–22.6	4.48

TABLE 2

Summary statistics for skull and dental dimensions of N. bifax *and* N. gouldi *from northern N.S.W. and far southeastern Qld*

All dimensions are in mm. Note that interbullae distance, bulla length and basicranial length were measured in occular units (1 unit = 0.082mm), and converted to mm

		N	MEAN	S.E.	S.D.	RANGE	CV
CONDYLOBASAL LENGTH	MALES						
	bifax	5	15.30	.13	.29	14.9–15.6	1.89
	gouldi	11	16.36	.11	.37	15.9–17.0	2.26
	FEMALES						
	bifax	6	15.68	.098	.24	15.4–16.0	1.53
	gouldi	8	16.46	.11	.32	16.1–17.0	1.94
GREATEST LENGTH	MALES						
	bifax	5	16.64	.14	.32	16.2–17.0	1.92
	gouldi	11	17.30	.13	.42	17.3–18.2	2.43
	FEMALES						
	bifax	6	16.93	.080	.20	16.6–17.1	1.18
	gouldi	8	17.91	.11	.32	17.5–18.4	1.79
CM^{1-3} LENGTH	MALES						
	bifax	5	6.22	.037	.084	6.1–6.3	1.35
	gouldi	11	6.57	.060	.20	6.3–7.0	3.04
	FEMALES						
	bifax	6	6.32	.054	.13	6.1–6.5	2.06
	gouldi	8	6.53	.041	.12	6.4–6.7	1.84

Table 2 (continued)

		N	MEAN	S.E.	S.D.	RANGE	CV
C^1-C^1 BREADTH	MALES						
	bifax	5	4.70	.032	.071	4.6–4.8	1.51
	gouldi	11	4.82	.055	.18	4.5–5.1	3.73
	FEMALES						
	bifax	6	4.93	.033	.082	4.8–5.0	1.66
	gouldi	8	4.86	.046	.13	4.6–5.0	2.67
ZYGOMATIC BREADTH	MALES						
	bifax	5	10.54	.11	.24	10.2–10.8	2.28
	gouldi	11	10.46	.10	.33	10.0–11.1	3.15
	FEMALES						
	bifax	6	10.73	.056	.14	10.5–10.9	1.30
	gouldi	8	10.60	.10	.28	10.1–10.9	2.46
INTERORBITAL CONSTRICTION	MALES						
	bifax	5	3.52	.037	.084	3.4–3.6	2.39
	gouldi	11	3.74	.028	.093	3.6–3.9	2.48
	FEMALES						
	bifax	6	3.52	.054	.13	3.3–3.7	3.69
	gouldi	8	3.75	.050	.14	3.6–4.0	3.73
BREADTH M^{3-3}	MALES						
	bifax	5	6.78	.058	.13	6.7–7.0	1.92
	gouldi	11	6.94	.049	.16	6.7–7.3	2.30
	FEMALES						
	bifax	6	7.07	.061	.15	6.8–7.2	2.12
	gouldi	8	6.91	.055	.15	6.7–7.0	2.17
BRAINCASE HEIGHT	MALES						
	bifax	5	6.36	.081	.18	6.1–6.6	2.83
	gouldi	10	6.34	.074	.24	6.0–7.0	3.78
	FEMALES						
	bifax	6	6.42	.040	.098	6.3–6.5	1.52
	gouldi	7	6.30	.058	.15	6.1–6.5	2.38
MASTOID BREADTH	MALES						
	bifax	5	8.80	.11	.25	8.4–9.0	2.84
	gouldi	11	9.23	.060	.20	9.0–9.6	2.17
	FEMALES						
	bifax	6	9.07	.080	.20	8.9–9.4	2.20
	gouldi	8	9.16	.082	.23	8.9–9.5	2.51
INTERBULLAR DISTANCE	MALES						
	bifax	5	2.13	.045	.10	2.0–2.3	4.69
	gouldi	10	1.61	.044	.14	1.4–1.8	8.69
	FEMALES						
	bifax	6	2.23	.026	.065	2.1–2.3	2.91
	gouldi	7	1.66	.057	.15	1.4–1.8	9.03
BULLAR LENGTH	MALES						
	bifax	5	3.59	.041	.092	3.4–3.7	2.56
	gouldi	10	4.06	.038	.12	3.8–4.3	2.95
	FEMALES						
	bifax	6	3.59	.039	.095	3.5–3.8	2.65
	gouldi	7	4.08	.053	.14	3.9–4.3	3.43
BASICRANIAL LENGTH	MALES						
	bifax	5	5.54	.067	.15	5.4–5.7	2.70
	gouldi	10	6.11	.060	.19	5.8–6.6	3.11
	FEMALES						
	bifax	6	5.76	.057	.14	5.7–6.0	2.43
	gouldi	7	6.00	.072	.19	5.7–6.3	3.17

The ranges of ear length for females of each species do not overlap; this separation is shown in Fig. 9. For the remaining nine external measurements however, there is extensive overlap between each sex of each species. For all external dimensions except ear length, the two species have similar mean values for equivalent sex. As there is nearly complete overlap in the ranges of forearm length between both species, a bivariate plot of ear length against forearm length (frequently used in bat systematics) is not useful for separating males of these species (Fig. 9).

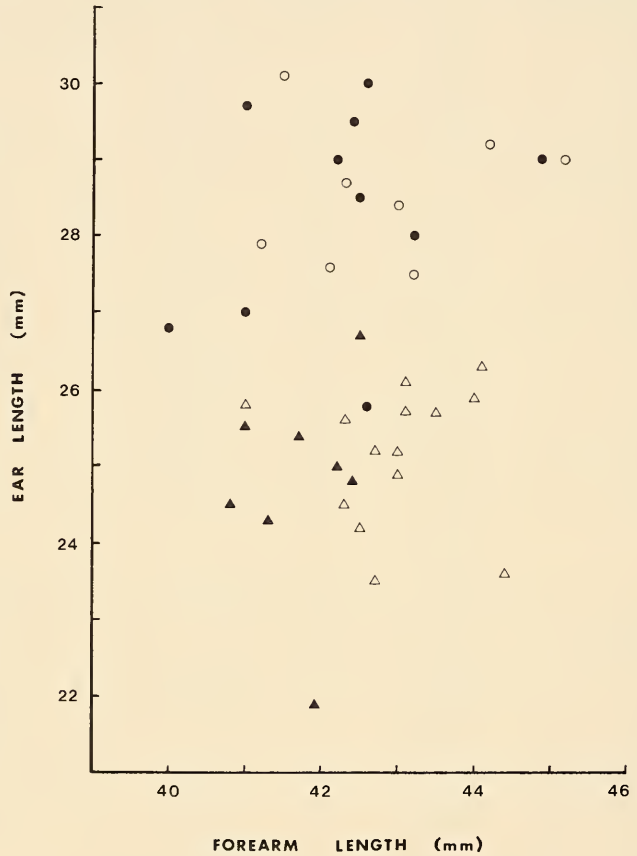

Fig. 9. Plot of ear length (mm) against forearm length (mm) for *N. gouldi* (circles) and *N. bifax* (triangles) from northern NSW and far southeastern Qld. Closed symbols represent males, open symbols females.

Skull dimensions overlap or abut in all but four characters: condylobasal length, greatest length of skull, interbullae distance and bulla length (Table 2). Clear separation of the two species results on a plot of zygomatic breadth against greatest length of skull (Fig. 10). Thus in terms of absolute size specimens of *N. gouldi* from northern New South Wales have longer skulls with bigger bullae. It remains to be seen whether these differences are maintained in larger samples.

Specimens of *N. gouldi* from this restricted region are more variable than *N. bifax* for the majority of external and cranial dimensions. This is reflected in sample coefficients of variation (see Tables 1 and 2), and is evident in a bivariate plot of zygomatic breadth against greatest length of skull (Fig. 10). This does not appear to be a site effect as

individuals from the same site have measurements at either end of the scatter for these characters. The significance of this, as well as the greater variation in the majority of other dimensions of *N. gouldi* is not evident at present. Until such variation is more clearly understood, it seems prudent not to test each species for statistically significant differences between character means.

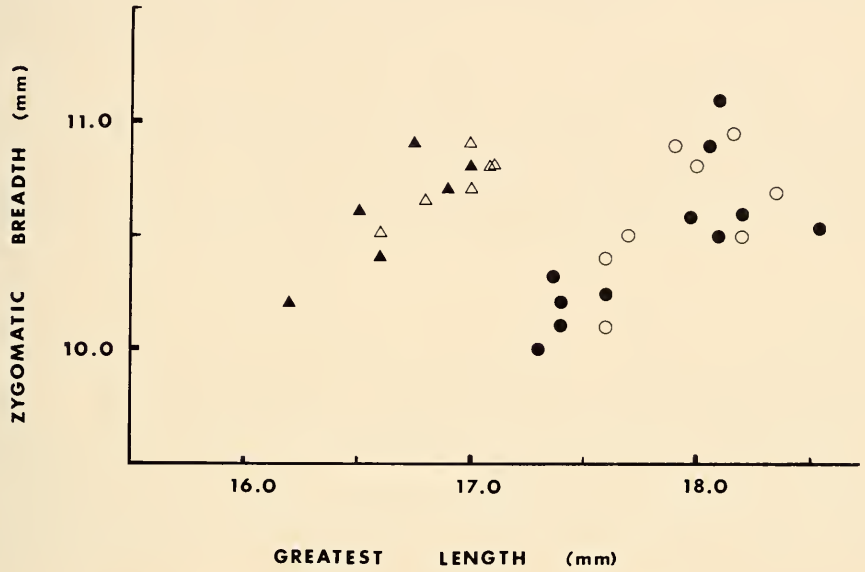

Fig. 10. Plot of zygomatic breadth (mm) against greatest length of skull (mm) for 19 *N. gouldi* (circles) and 12 *N. bifax* (triangles) from northern NSW and southeastern Qld. Males represented by closed symbols, females by open symbols.

Discussion

There is little doubt that in eastern Australia, *N. gouldi* and *N. bifax* are distinct taxa. In the original description of *N. bifax*, Thomas distinguished it from *N. gouldi* by its relatively shorter ears, smaller bullae, more reduced post-nasal bump, and by the distally bifurcate baculum (compared to the simple point of *N. gouldi*). This study supports the validity of all of these criteria.

Based on specimens pooled from different localities, ranges for each species overlap for the majority of external and skull dimensions. Pooling localities, however, could obscure size differences that might exist between species at a single locality. Specimens pooled from a restricted geographic area (northern New South Wales and southeastern Queensland) were collected from a particularly diverse range of environments, but either sex of the two species could be separated using some dimensions. Adequate samples of both species from a single locality are obviously required to analyse this situation further but are not currently available.

Skulls of either sex of both species are separable on the basis of interbullae distance irrespective of locality, this character being a reflection of bullae size, a further distinguishing feature. This is significant given the extent of within-species variation and that when specimens are pooled from all localities ranges of all other dimensions examined

overlap between species. This apparently reflects differences in the auditory capabilities of each species though audition in either species is little known.

As well as being broadly sympatric over a large part of their respective range, *N. bifax* and *N. gouldi* have been captured together at the same site in a number of areas. Both species were trapped at the same site in the same evening at a number of localities in northern New South Wales (Parnaby, 1986). *N. bifax* was captured frequently at near coastal localities up to 300m in elevation. By contrast, *N. gouldi* was captured in much lower numbers but at sites ranging from near sea level (such as at Broken Head Nature Reserve) to 1120m at Bar Mountain in the Tweed Range. Churchill (*pers. comm.*) captured both species at the same site in the same evening at Mt Leysham near Charters Towers, north Queensland.

I know of only three specimens of *N. gouldi* from the Atherton region, which at present represent the most northern record for this species. Cairn and Grant collected two females (AM M7024-25) from the Herberton area in 1889 while the third specimen (QM JM5381, also female) was captured in a harp trap set near a stream in dry sclerophyll forest at Atherton. Richards (1984) did not detect this species during an extensive bat survey of north Queensland rainforests, which included the Atherton region, while he found *N. bifax* to be abundant. A variety of techniques were used but he relied principally on identification of free flying bats by electronic monitoring of echolocation calls. Although more effort was concentrated on rainforest, sclerophyll forest and woodland were also sampled (Richards, *pers. comm.*). Thus *N. gouldi* appears to be uncommon in the Atherton region where it is possibly restricted to schlerophyll forest.

Electrophoretic evidence based on samples of each species taken in sympatry at several localities in northern New South Wales indicates clearly that they are good biological species. In addition, electrophoretic profiles between each species are such that hybrids between them would be readily detected (M. Adams and P. Baverstock, *pers. comm.*). However, only a small number of individuals of each species have been examined electrophoretically from areas of known sympatry.

The affinities of a number of populations variously referred to *N. gouldi*, *N. bifax* and *N. timoriensis* require clarification. Churchill *et al.* (1984) describe specimens of a *Nyctophilus* occurring sympatrically with *N. geoffroyi* and *N. bifax* from Mt Leysham, south of Charters Towers and while noting the similarity with *N. gouldi*, they were unable to allocate these animals to any known form of *Nyctophilus*.

I have examined these specimens (Queensland Museum numbers JM5248 and JM5358, not JM4361 and JM4362 as stated by Churchill *et al.* (1984), which are comparable with material from other areas of central Queensland. In view of the considerable size variation amongst *N. gouldi* from different localities, which appears to reflect local environmental conditions, there seems to be no reason for distinguishing these animals from *N. gouldi*.

A further question concerns the nature of the relationship between *N. bifax bifax* and *N. bifax daedalus*, and their distribution in north Queensland. These taxa are morphologically distinct and both could occur in the Gulf region of northwest Queensland, although sympatry has not been demonstrated. Churchill *et al.* (1984) record *N. bifax* from the Lawn Hill area. Although they did not distinguish *N. bifax bifax* from *N. bifax daedalus*, a specimen from Lawn Hill lodged by them in the Queensland Museum (JM5246) is clearly referable to *N. b. daedalus*. Of the material I have examined, the most western record of *N. bifax bifax* in Queensland is a specimen (AM M13356) from Einasleigh River (18° 11′S, 144° 00′E), west of Mt. Surprise.

McKenzie *et al.* (1977) identified a specimen of *N. bifax* from the Drysdale River National Park, northern Western Australia. They assigned this specimen (WAM M14097) to *N. b. bifax* rather than *N. b. daedalus*, on the basis of its bifurcate baculum. I

have examined this specimen and believe that it is distinct from *N. b. bifax*; in bacula and dental features it is closest to *N. b. daedalus*. Thus with the possible exception of a specimen in the British Museum from Cloncurry (Thomas, 1915) which I have not examined, I am not aware of any definite record of *N. b. bifax* west of that collected from the Einasleigh River.

The status of *N. bifax daedalus* remains confused. The arrangement of Johnson (1964) is usually followed. He regarded it as the western race of *N. bifax* though its affinities have also been placed with *N. gouldi* by Troughton (1941) (as *N. timoriensis gouldi*) and Koopman (1984). Although the affinities of *daedalus* remain unclear, it does not appear to belong with *N. bifax*.

Large *Nyctophilus* from Tasmania have variously been referred to both *N. gouldi* and *N. timoriensis*. Hall and Richards (1979) record *N. gouldi* from Tasmania for the first time. The basis of this record (Richards, *pers. comm.*) is a specimen from Flinders Island, registered in the Queen Victoria Museum (reg. number 1978.1.351). In skull and baculum shape, it resembles a large version of mainland *N. geoffroyi*, and is unlike Victorian *N. gouldi*. Thus, I am not aware of any valid record in the literature of *N. gouldi* from Tasmania; the relationships of Tasmanian *Nyctophilus* require clarification.

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Appendix 1

SPECIMENS EXAMINED

All the following specimens have been examined by the author. A subset of these has been measured and details are available from the author.

Nyctophilus gouldi

Queensland. Atherton, 17° 16′S, 145° 29′E: lf (JM5381); Herberton, *ca* 17° 23′S, *ca* 145° 23′E: 2f (AM M7024-25); Mt Leysham, 20° 15′S, 146° 15′E: 2m,lf (QM JM5248, JM5358, AM M12967); Finch Hatton, 21° 09′S, 148° 38′E: lf (QM JM1113); Capella, 23° 05′S, 148° 01′E: 2m (AM M6312-13); Retro Downs Stn, Capella, 22° 52′S, 147° 54′E: 8m,lf (QM JM6184-85, JM6218-21, JM6301-03); Craigmore, 23° 55′S, 147° 53′E: lf (QM JM2946); Blackdown Tableland, Mimosa Ck, 23° 47′S, 149° 05′E: lf (QM JM5359); Pluto Timber Reserve, via Tambo, *ca* 25° 00′S, *ca* 147° 05′E: l(unsexed) (CM15593); Mt Pluto, 3km E, 25° 00′S, 147° 05′E: lm (CM4393); Mt Moffatt, 225km N of Mitchell, 25° 01′S, 147° 57′E, lm (QM J20378); Mitchell, 26° 29′S, 147° 58′E: lm (CM2334); Babbiloora Stn, 25° 12′S, 147° 57′E: 4m (JM5360-5363); Moolangool Stn, via Gin Gin, *ca* 24° 45′S, *ca* 151° 32′E: 2f (AM M5972, M6096(imm.)); Hervey Bay, *ca* 25° 06′S, *ca* 152° 49′E: 2f (QM JM2577, JM2596); Chinchilla, *ca* 26° 44′S, *ca* 150° 36′E: lm,lf (AM M7634, QM J1763); Chinchilla, 32km SW, *ca* 26° 55′S, *ca* 150° 25′E: lm (QM JM506); Conondale Rge, *ca* 26° 39′S, *ca* 152° 38′E: lf (AM JM5364); Pomona, 26° 22′S, 152° 52′E: lm (QM JM991); Millmerran, 27° 53′S, 151° 16′E: lm,lf (AM M3911-12); Caloundra, 26° 48′S, 153° 08′E: lf (QM J1762); Moggil Forest, 2f (QM JM5365-5366); Wallangara, 28° 55′S, 151° 56′E: lm (AM M11841); Levers Plateau, NW edge, 28° 19′S, 152° 51′E: lm,lf (AM M13411-12); North Tamborine, 27° 56′S, 153° 11′E: lm (QM J7095); Brisbane, 27° 28′S, 153° 01′E: lm (QM J10872).

New South Wales. Tweed River, Tyalgum 28° 22′S, 153° 12′E, lf (AM M5450); Tweed Range, Paddys Mountain Tk, 28° 25′S, 153° 07′E: 2m (AM M13171, M13392); Tweed Range, Bar Mountain picnic area, 28° 27′S, 153° 19′E: lm (AM M13403); Tweed Range, Airdrop Rd, 28° 24′S, 153° 03′E: 2m (AM M13393, M13406); McPherson Rge, Palm Gully area, 28° 22′S, 152° 55′E: lm,lf (AM M13178, M13181); Tooloom, 28° 37′S, 152° 25′E: lm,lf (CM573-574); Big Scrub Flora Reserve, 28° 38′S, 153° 20′E: lm (AM M13243); Terania Ck, Nightcap National Park, 28° 34′S, 153° 17′E: lf (AM M13235); Whiam Whiam State Forest, 28° 35′S, 153° 22′E: lm,2f (AM M16029-16030, M14184); Broken Head Nature Reserve, 28° 33′S, 153° 37′E: lm,lf (AM M13380, M13389); Woolgoolga Nature Reserve, 30° 07′S, 153° 09′E: lm,2f (AM M13227-28, M13231); Dorrigo National Park, 30° 22′S, 152° 48′E: 2m (AM M13197-98); New England National Park, 30° 30′S, *ca* 152° 27′E: 2m,2f (AM M13200, M13202, M13208, M13213); Moree, 29° 28′S, 149° 51′E: lf (AM M5956); Pilliga Scrub, *ca* 31° 00′S, *ca* 149° 30′E: lm,lf (AM M5968, M8471); Pilliga Scrub, 30° 32′S, 149° 32′E: 3f (AM M16023-16025); Spear Ck, 7km E of Apsley Rv., 30° 55′S, 152° 05′E: lf (AM M14189); Mt Boss State Forest, 31° 11′S, 152° 27′E: 4m,2f (AM M14108-M14113); Mooraduck Ck, Werrikimbie National Park, 31° 09′S, 152° 13′E: lm (AM M12548); Doyles River State Forest, 31° 27′S, 152° 10′E: lm,4f (AM M14114-M14118); Sea Acres Nature Reserve, Port Macquarie, 31° 28′S, 152° 56′E: lf (AM M13434); Gloucester Tops, 3.8km WNW, 32° 02′S, 151° 34′E: lm,3f (AM M13425-26, M13429, M13432); Upper Allyn via Eccleston, 32° 10′S, 151° 29′E: lm (AM M9394); Canningalla Stn,

7 ml NW of Dungog, 32° 24′S, 151° 45′E: lf (AM M10002); Weabonga, 31° 13′S, 151° 19′E: lf (AM M7631); Wheogo Stn, 20km N of Dunedoo, *ca* 31° 50′S, *ca* 149° 24′E: lm,lf (AM M4284-4285); Turee, 31° 56′S, 149° 48′E: lm (AM M3746); Munghorn Gap, NE of Mudgee, 32° 25′S, 149° 50′E: 2m,2f (AM M14104-M14107); Bulahdelah, 8km SE, 32° 25′S, 152° 12′E: lm (AM M10312); Olney State Forest, 33° 06′S, 151° 18′E: 16m,10f (AM M15980-15989, M16007-16022); Anna Bay, S of Port Stephens, 32° 46′S, 152° 04′E: 2f (AM M4273, M4321); Wyong Ck, 33° 10′S, 151° 19′E: lf (CM1575); Ourimbah, 33° 22′S, 151° 22′E: lm (AM M4224); Gosford, 33° 26′S, 151° 20′E: 4f (AM M4433-4436); Ash Island, Hunter River, 32° 51′S, 151° 43′E: lm (AM M2566); Dangar Island, 33° 32′S, 151° 14′E: lm (AM M9265); Sydney area: Botany, lm (AM M2564); Carlingford, lm (AM M7618); Eastwood, lf (AM M8014); North Wahroonga, 33° 42′S, 151° 07′E: lm (AM M9191); Gymea Bay, lm (AM M7482). Hazelbrook, 33° 44′S, 150° 27′E: lm,2f (AM M3041, M3545, M3739); Lawson, 33° 43′S, 150° 26′E: lf (AM M1437); Abercrombie, Arch Cave, 33° 55′S, 149° 22′E: lf (CM2323); Jenolan Caves, 33° 49′S, 150° 02′E: lf (AM M1702); 3km S of Coco Ck Cave, Capertree Valley, *ca* 33° 08′S, 150° 10′E: lm (AM M9846); Junction of Capertree Rv. — Wolgan Rv., 33° 12′S, 150° 28′E: lm,lf (AM M11481-11482); Cob area, Culoul Rge, *ca* 33° 13′S, *ca* 150° 36′E: lm (AM M11632); Grassy Hill Tk., W of Putty Rd., *ca* 33° 22′S, *ca* 150°41′E: lm (AM M11090); Millamalong, nr. Mandurama, 33°15′S, *ca* 150° 40′E: lf (AM M3414); Pheasants Nest nr. Picton, 34° 15′S, 150° 40′E: lm (AM M11557); Campbelltown, 9km S, 34° 08′S, 150° 47′E: lm (AM M14088); Berrima, 34° 29′S, 150° 20′E: lm (AM M3436); Robertson, 34° 35′S, 150° 35′E: lf (AM M6272); Carrington Falls, 34° 38′S, 150° 41′E: lf (CM4588); Mt Keira, 34° 24′S, 150° 51′E: 2m (AM M9140, CM4587); Keiraville, 34° 25′S, 150° 50′E: lm (CM4589); Bungonia Caves, 34° 52′S, 149° 57′E: lf (AM M7638); Narooma, 36° 13′S, 150° 09′E: lf (CM1745); Jervis Bay Nature Reserve, 35° 09′S, 150° 43′E: lm,2f (AM M13438-13440); Sussex Inlet, 35° 12′S, 150° 33′E: lm (AM M14188); Araluen, 35° 39′S, 149° 49′E: lf (CM612); Mogo, 35° 47′S, 150° 09′E; lm (CM1895); 1.4km E of Wollybut Tk.. Mumbulla State Forest, 36° 33′S, 149° 52′E: lm (AM M12752); Argalong, 35° 18′S, 148° 24′E: lm (AM M4534); Tumut State Forest, 35° 22′S, 148° 12′E: lm (AM M11300); Yarrangobilly Caves, 35° 39′S, 148° 28′E: lm (CM6295); Murrumbateman, 34° 58′S, 149° 02′E: lf (CM4705); Sutton, 35° 10′S, 149° 15′E: lm (CM1457); Mt Tindery, 35° 42′S, 149° 16′E: l (CM2062); Temora, 9km W, 34° 35′S, 147° 25′E: lf (AM M11716); Temora, 15km SW, 34° 31′S, 147° 22′E: lm,lf (AM M13576-77); The Rock Nature Reserve, 35° 16′S, 147° 04′E: lm (AM M11522); Wagga Wagga, Livingstone State Forest, 35° 25′S, 147° 25′E: 2m,2f (AM M11217, M11521, M11655, M11717); Gerogery, 35° 50′S, 147° 00′E: lm (CM4029); Wahgunya State Forest, 35° 51′S, 145° 59′E: lm (AM M11494); Deniliquin, 35° 32′S, 144° 57′E: lm (MV C5159).

Australian Capital Territory. Captains Flat, 35° 35′S, 149° 27′E: lm (CM4747); Bushrangers Ck, Brindabella Rge, lm (CM4361); Canberra, 13km N, 35° 17′S, 149° 13′E: 2m (CM2382, CM2387); Lake Burley Griffith, 35° 17′S, 149° 13′E: lm,2f (CM2345, CM2386, CM2434); Black Mountain, 35° 16′S, 149° 06′E: lm (CM2077); Yarralumla, lm (CM591).

Victoria. Junction Little Bog Ck-NSW border, 37° 19′S, 149° 05′E: lm (MV C26595); Boundary Road, Wingham River, 37° 42′S, 149° 28′E: lf (C24907); Mitta Mitta, 36° 32′S, 147° 22′E: lm (CM4359); Mt Buffalo National Park, 36° 45′S, 145° 48′E; lm,3f (MV C26957-26960); Myrtleford, 24km S, 36° 45′S, 146° 44′E: lf (MV C11467); Bogong 36° 48′S, 147° 13′E: lm,lf (MV C11565-11566); Dargo, 30km NNW, 37° 11′S,

147° 12′E: 2m,1f (MV C26961-26963); Nathalia, Goulburn River, 36° 10′S, 145° 06′E: 1m (MV C25643); Mt Warby, 1.6km NNW, 36° 20′S, 146° 12′E: 2m (MV C25671-25672); Balook, 38° 26′S, 146° 34′E: 1f (MV C26952); Mt Killawarra, 36° 09′S, 146° 14′E: 1m (MV C25657); Edi, 4km WNW, 36° 38′S, 146° 24′E: 1m,3f (MV C25186-25187, C25194); Mt Macedon township, 37° 25′S, 144° 34′E: 1m (MV C7452); Daylesford area, 37° 21′S, 144° 09′E: 4f (MV C16020-16021, C16152, C26951); Maroondah Reservoir, 37° 38′S, 145° 35′E: 2m (MV C26968); Croydon, 37° 48′S, 145° 17′E: 1m,1f (MV C5419, C25476); Jindivick, 3km NNW, 38° 00′S, 145° 52′E: (MV C24907); Refuge Cove, Wilsons Promontory, 39° 03′S, 146° 28′E: 1m (MV C17129); Mt Erica, 7.1km SSW, 37° 53′S, 146° 21′E: 8m,1f (MV C25350, C25355, C25360, C25366-25367, C25372, C25374, C25386); Mt Baw Baw, 5.8km SSW, 37° 50′S, 146° 17′E: 1f (MV C25336); Willow Grove 38° 05′S, 146° 11′E: 1m (MV C25324); Nowa Nowa area, 37° 16′S, 147° 58′E: 1m,2f (MV C26093-26094, C26096); Bruthen, 8km NW, 37° 39′S, 147° 46′E: 1m,1f (MV C26965-26966); Lockup Ck, Waratah Spur Tk. 37° 24′S, 149° 06′E: 1f (MV C25905); Yalmany Rd, Roger Rv., 37° 18′S, 148° 35′E: 5m,1f (MV C25934-25939); Cooagalah block, 37° 24′S, 149° 21′E: 2m,2f (MV C25969-25972); Mt Noorinbee, 6km NNW, 37° 27′S, 149° 05′E: 1f (MV C26964); Cann River, 37° 34′S, 149° 10′E: 1m (MV C22278); Bemm River, 37° 45′S, 148° 58′E: 1m (MV C11434); Mt Ellery, 1.7km W, 37° 24′S, 148° 47′E: 1m,1f (MV C26409-26410); Teddington Reservoir, 1.5km S, 36° 52′S, 143° 16′E: 5m,6f (AM M16750, MV C26968-26978); Zumstein, 37° 05′S, 142° 22′E: 1m (MV C26967); Mt Rosea, Grampians State Forest, 37° 12′S, 142° 30′E: 1f (MV C25691); Mt Eccles National Park, 38° 05′S, 142° 00′E: 1m (MV C2605); Napier Forest, 37° 54′S, 142° 04′E: 1m (MV C23676); Otway Ranges, 38° 41′S, 143° 36′E: 3m,1f (MV C26953-26956); Grey River Scenic Reserve, nr. Kennett River, 38° 40′S, 143° 51′E: 1f (MV C25343); Irrewillipe, 38° 25′S, 143° 25′E: 1m (MV C17906).

Nyctophilus bifax

Queensland. Moa Island, 10° 11′S, 142° 16′E: 1f (MV C8800); Prince of Wales Is., *ca* 10° 41′S, *ca* 142° 09′E: 2m,1f (CM11632-34); Lockerbie Scrub, 10° 48′S, 142° 27′E: 4m,2f (CM11626-31); Carnegie Rge, Cape York, 10° 46′S, 142° 31′E: 1f (QM JM5367); Captain Billy Ck. 11° 37′, 142° 50′E: 2m,3f (QM JM5368-5372); Iron Range, 12° 43′S, 143° 19′E: 2m,1f (QM JM5373-5375); Iron Range, 12° 45′S, 143° 12′E: 4m,2f (AM M16188-16193); Archer River, 13° 27′S, 142° 57′E: 1m (QM JM5376); Archer River, 5km S, 13° 29′S, 142° 58′E: 2m,2f (AM M12958-12959, M16032-16033); Peach Ck, McIlwraith Rge, 13° 40′S, 143° 07′E: 2m,1f (QM JM5377-5379); Buthen Buthen, Cape York, 13° 21′S, 143° 28′E: 1m,2f (QM JM2429-30, JM2475); Rocky River, *ca* 13° 48′S, *ca* 143° 27′E: 1m (CM4486); Station Ck, 16km S of Coen, 14° 03′S, 143° 16′E: 2f (AM M13352, M13369); Cooktown, Jones Lagoon, 15° 26′S, 145° 10′E: 1m,1f (AM M12956-12957); Cooktown, Walker Bay, 15° 31′S, 145° 17′E: 1f (AM M12955); Bloomfield, 15° 56′S, 145° 21′E: 1m (AM M11278 imm.) Cape Tribulation, 16° 10′S, 145° 25′E: 5m,2f (AM M13344-50); Kewarra Beach, 18km N of Cairns, 16° 37′S, 145° 41′E: 1m (AM M17301); Clump Point, Tully, 17° 52′S, 146° 07′E: 1f (AM M8386); Kuranda, 16° 49′S, 145° 38′E: 2m (CM15043, QM J4409); Atherton, 17° 16′, 145° 29′E: 6m,2f (QM JM5380, JM5382, AM M13602-13605, M13611-13612); Severin Creek State Forest, Atherton Tableland, 17° 11′S, 145° 40′E: 3m,4f (AM M16183, M16185-16187, QM JM5401-5403); Wongabel State Forest, Atherton Tableland, 17° 19′S, 145° 29′E: 1m,3f (AM M16181-16182, M16184, QM JM5404); Herberton district, *ca* 17° 23′S, *ca* 145° 23′E: 1m,2f (AM M557-58, M560); Chillagoe, 17° 09′S, 144° 31′E: 1m (CM5891); Einasleigh River, Kennedy Highway, 18° 11′S, 144° 00′E: 1m (AM

M13356); Ravenshoe, *ca* 17° 36′S, *ca* 145° 29′E: lm (AM M8011); Innisfail, 17° 32′S, 146° 01′E: lm,lf (CM4834, AM M8005); Cardwell, Kirrama State Forest, *ca* 18° 10′S, *ca* 145° 40′E: lf (QM JM5383); Mt Spec, 64km N of Townsville, 18° 56′S, 146° 11′E: lf (CM4835); Palm Is., 18° 40′S, 146° 33′E: lf (QM J5274); Fanning River Stn, 19° 16′S, 146° 49′E: lm (QM JM5262); Charters Towers, 18km E, 20° 06′S, 146° 26′E: 2m (AM M13353-54); Charters Towers, Mt Leysham, 20° 15′S, 146° 15′E: lm (QM JM5384); Eungella, 21° 08′S, 148° 29′E: lm (AM M11175); East Funnell Ck, nr. Sarina, *ca* 21° 33′S, *ca* 149° 09′E: 2f (AM M7038-39); Minga Mountain, Byfield, 22° 52′S, 150° 32′E: lm (QM JM5385); Rockhampton, 23° 22′S, 150° 32′E: (QM JM5386); Hervey Bay, *ca* 25° 06′S, *ca* 152° 49′E: 2f (QM JM2571, JM2574); Noosa Heads, 26° 23′S, 153° 07′E: l(?sex) (MV M15368); Conondale Rge, *ca* 26° 39′S, *ca* 152° 38′E: lm (QM JM5387); Mt Nebo, 27° 24′S, 152° 47′E: lm (QM JM5388).

New South Wales. Reserve Ck, Murwillumbah, *ca* 29° 39′S, *ca* 150° 43′E: lm (CM4743); Billinudgel Swamp, 28° 29′S, 153° 32′E: lm,3f (AM M14090-14093); Brunswick Heads Nature Reserve, 28° 33′S, 153° 33′E: lm (AM M13388); Broken Head Nature Reserve, 28° 33′S, 153° 37′E: 5m,2f (AM M13378, M13381-83, M13385-87); Broken Head area, 28° 44′S, 153° 36′E: lf (AM M15330); Whiam Whiam State Forest, 28° 35′S, 153° 22′E: lf (AM M16031); Nightcap National Park, Terania Ck, 28° 34′S, 153° 17′E: lf (AM M13234); Big Scrub Flora Reserve, 28° 38′S, 153° 20′E: 2m,2f (AM M13240, M13247-M13249); Iluka Nature Reserve, 29° 24′S, 153° 22′E: 2m,lf (AM M13191-M13192, M13232).